the abdominal segments, the piceous antennae, tibiae and tarsi, and the green femora. In contrast with Vollenhoven's type, the species *spectabilis* differs in being more convex and more glossy dorsally, with finer puncturation, as well as being entirely differently colored. The distinguishing characteristics that set this new species off from others in the genus are the striking yellow and black contrasting combination of colors, the incised nature of the apex of the head, and the very large topaz ocelli.

NOTES ON POMPILID WASPS THAT DO NOT DIG BURROWS TO BURY THEIR SPIDER PREY

By B. J. Kaston[1]

For a number of years, in the course of collecting and studying spiders themselves, I have been accumulating data on spider parasites. Brief articles on dipterous and mermithid parasites have already been published by me (Kaston, 1937, 1945) but as yet my notes on the hymenopterous parasites have not been completed.

The best known and most commonly reported parasites are the ichneumons belonging to *Polysphincta* and related genera. The larva of the parasite can be seen attached to the outside of the spider's body, in most cases on the abdomen of the host. This is in marked contrast to the situation when the parasite is a dipteron, whose larva feeds *within* the body of its host. Consequently, any spider found with a larva, or the egg of a parasite, on the outside of its body was assumed by me to be parasitized by an ichneumon. In many cases, because of the small size of the parasite the spider was not saved alive at the time of collection, since the parasite was not then noticed. In such cases the parasite would come to my attention only when the spiders were brought out later for study, after they had been preserved in alcohol. In other cases, even though the spider and its parasite may have been kept alive in the laboratory for a time, I was unsuccessful in rearing the parasite to maturity. One that I did succeed in rearing turned out to be, much to my astonishment, not an ichneumon, but a pompilid wasp.

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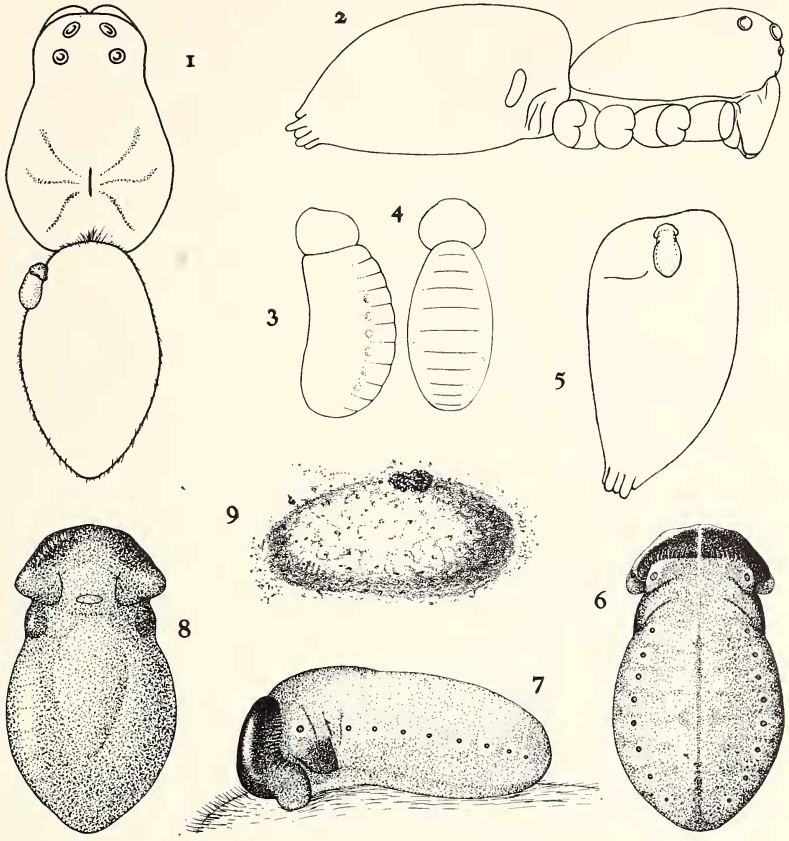
[1] Central Connecticut State College, New Britain, Conn.

Now, I had known of pompilid wasps stinging spiders and carrying them off to be buried. Although a few exceptions to this behavior have been known for many years for the Old World fauna, it is only recently that we have come to learn that comparable cases occur in the New World too, and they are less rare than previously supposed. In effect, a non-sedentary spider (most often a lycosid) may be parasitized in the manner of a *Polysphincta,* where the host quickly recovers from the wasp's sting, and continues to run about, apparently normally, for an extended period of time. The discovery that a pompilid wasp, and not an ichneumon, may be the parasite prompted me to recheck my notes, with a view to finding other instances. I was able to find ten other cases, although in these the parasite was not reared. Except for one case the spiders were all collected by myself. I have been stimulated to prepare my notes for publication by the extensive studies of Krombein, and of Evans. The latter's essay on the comparative ethology of spider wasps (1953) is a particular interesting and valuable contribution to this field.

Report of Cases of Pompilid Parasitism

No. 1. The spider, a young lycosid (my number 957) was collected at Gainesville, Georgia, on May 14, 1945. Attached to the right side of its abdomen was a small grayish-white larva. Upon returning to the laboratory the spider was placed in a small container, with the expectation of rearing the parasite. Examination on the following day revealed no change, but on May 16th at 8: 30 A.M. I found that the spider had succumbed during the night preceding and the larva, now greatly enlarged, was engaged in consuming the remains of the corpse. By 3: 30 P.M. it appeared to have completed its feeding, and at about 8: 30 P.M. the larva began to spin its cocoon. By 8: 30 the following morning the cocoon was completed. It was elliptical, 9.1 mm. long, 4.1 mm. at its widest diameter, and was transparent enough at first so that movements of the prepupa could be discerned within. The cocoon later changed to opaque silvery-brown, and here and there over the surface, in amongst the long threads, could be seen brown specks which were fragments of the spider's cuticle that the larva had incorporated in the structure. By the next day it had pupated, and one end of the cocoon appeared dark because of the meconial discharge showing through (Fig. 9). The imago, a male, emerged on June 9, after cutting a circular "lid" at the top of the cocoon. It was subsequently identified by H. Townes as *Minagenia osoria* (Banks).

No. 2. The spider, a very young lycosid (my number 946)



Explanation of Plate

Fig. 1. Dorsal aspect of *Lycosa frondicola* #912, showing the parasite larva attached to the left side of the spider's abdomen. Fig. 2. *Lycosa punctulata* #838, from the right side, showing egg of parasite. Fig. 3. Lateral aspect of newly hatched larva on #838. Fig. 4. Dorsal aspect of newly hatched larva on #838. Fig. 5. Abdomen of *Lycosa frondicola* #856, from the left, showing parasite larva. Fig. 6. Dorsal aspect of parasite from #856. Fig. 7. Lateral aspect of parasite from #856. Fig. 8. Ventral aspect of parasite from #856. Fig. 9. Pupal cocoon of *Minagenia osoria* (Banks) #946.

was collected at Gainesville, Georgia, on September 19, 1940, and brought into the laboratory for rearing of the parasite. As in the preceding case, there was a small grayish-white larva attached to the right side of the abdomen. For the next three and a half months the spider behaved normally, molting on September 29, October 13, November 4, and November 19. I observed that each time the spider molted it failed to shed the portion of its cuticle where the parasite was attached.

On December 16 I noticed that the larva, which up to then had grown hardly at all, now appeared to be considerably inflated. While previously the head had been relatively quite wide the greatly increased size of the trunk segments made the head now appear relatively narrower. On the evening of December 18 the parasite appeared to be beginning a molt, with the old cuticle splitting at the anterior region. By 6 P.M. on December 19 the exuviae had been pushed back to the posterior end. In this instar the parasite's head was relatively much narrower than in the previous one. During the next few days the parasite grew steadily larger, but the spider did not appear in the least inconvenienced. I had this spider and parasite with me at the Christmas meetings of the entomologists in Philadelphia, and showed the specimens to ichneumonologists R. A. Cushman and H. D. Pratt. Neither one could recognize the parasite, nor even venture a suggestion as to the group to which it belonged.

On the morning of January 1, 1941 I found that the parasite had molted again during the preceding night, and by 10:30 A.M. the spider appeared dead. By 3 P.M. the larva had completely consumed the spider's abdomen, and by 4:30 the cephalothorax and legs too. At midnight, the larva, now about 8 mm. long, began spinning its cocoon. At 9 A.M. on January 2 the cocoon was complete, about 8.5 mm. long by 4 mm. at its widest diameter. It was quite similar to that described for #957 (above) including the bits of spider débris strewn about on the outside (Fig. 9). Unfortunately the specimen failed to emerge, but on opening the cocoon in July I found a fully developed and fully pigmented male. Apparently it had died quite close to the time for it to emerge. It was subsequently determined by H. Townes (1957) as the same species as my #957.

Since this parasite had been collected in an early instar, and I had noted especially its peculiarly wide head, it occurred to me to look through my other parasite material for similar larvae (which had been preserved). Several were found and in each case the host turned out to be a non-sedentary, running spider. It seems obvious

that all these likewise represent cases of parasitism by pompilids.

No. 3. The spider, a mature female *Lycosa punctulata* Hentz (my number 838) was collected by me at Killingworth, Connecticut, on June 23, 1935. It was seen to have the egg of a parasite attached to the right side of its abdomen (Fig. 2), and so was kept alive in the laboratory. The egg measured 1.5 mm. in length and 0.54 mm. at its widest diameter. The upper pole was a pale translucent pearly gray, the lower pole faintly yellow, and the remainder, white. On June 26 the gray area extended down to occupy the upper third of the egg.

On June 27 the larva appeared to have hatched and it could be seen that the head was white, and rather sharply set off (Figs. 3 and 4). It was possible to make out 11 brownish segments, the three thoracic and eight abdominal. Of these latter the last two were very indistinct, and the first six bore faint indications of paired spiracles. On June 28 the larva was 2.25 mm. long and 0.92 mm. wide. Unfortunately I accidentally injured the larva in handling the specimens and it died.

No. 4. The spider, a mature female *Lycosa frondicola* Emerton (my number 881) was collected at Bethany, Connecticut, on September 25, 1937. Attached to the right side of the abdomen, near the venter, was an elliptical white egg measuring 2.1 mm. in length and 0.75 mm. at its greatest diameter. On September 27 the egg hatched, and as in the preceding case (#838 above) the larva showed a white head, well set off from the darker body. On September 29 at 9 A.M. it was found that the larva had dropped off the spider and was dead.

No. 5. The spider, a young male *Schizocosa saltatrix* (Hentz) (my number 345) was collected at Southbury, Connecticut, on April 30, 1933. It was bearing a small grayish-white larva attached to the left side of the abdomen. The spider molted on May 26, and again on June 13 (to maturity). It remained alive until July 21, and in all this time no change in the size of the parasitic larva was detectable.

No. 6. The spider, a male *Pisaaurina mira* (Walckenaer) (my number 883) was collected at Roxbury, Connecticut, on September 26, 1937. On the right side of its abdomen was a small grayish-white larva. The spider died on September 28.

The remaining cases to be cited are those in which the parasite was not noticed when the spider was collected, but only when the spider was taken out of preserving alcohol for study.

No. 7. The spider, a nearly mature female *Lycosa frondicola* Emerton (my number 856) was collected at West Ossippee, New Hampshire, on July 25, 1936. Attached to the left side of the abdomen was a parasite larva (Figs. 5, 6, 7, 8). It was 1.1 mm. long and 0.6 mm. at the widest part of the abdomen. The head was quite well set off, dark and shiny. The segments of the trunk were faintly indicated, and a pair of spiracles could be seen on the prothorax as well as on the eight abdominal segments.

No. 8. The spider, a young female *Schizocosa saltatrix* (Hentz) (my number 857) was collected at Mt. Carmel, Connecticut, on April 19, 1935. A parasite larva exactly like that of #856 (above) was attached in the same position on the spider's abdomen. However, this larva was smaller, being only 0.7 mm. long and 0.39 mm. wide.

No. 9. The spider, a young female *Schizocosa saltatrix* (Hentz) (my number 861) was collected at Wilsonville, Connecticut, on April 18, 1937. The parasite larva looked exactly like those of #856 and #857 (above) but was attached on the right side of the spider's abdomen, instead of the left. It measured 0.84 mm. in length and 0.45 mm. in width.

No. 10. The spider, a young female *Lycosa frondicola* Emerton (my number 912) was collected at Mt. Carmel, Connecticut, on September 3, 1939. The parasite larva looked exactly like those on #856, #857, and #861 (above) and was on the left side of the spider's abdomen (Fig. 1). It measured 0.82 mm. in length and 0.43 mm. in width.

No. 11. The spider, a young lycosid (my number 976) was collected by H. W. Levi in Pitkin County, Colorado, on July 20, 1954. It was carrying an ellipsoidal white egg fastened to the right side of its abdomen. The egg measured 1.75 mm. in length and 0.6 mm. at its greatest diameter.

Discussion and Review of the Literature

In theorizing on the evolution of pompilid habits Emery (1894) suggested that the original members of this family merely fastened an egg on to the body of the prey but left the latter where they found it instead of dragging it off to bury it. Others, including Iwata (1942) have likewise implied that this is a primitive type of behavior. But Evans (1953) has given good reasons for believing, rather, that this trait of not burying the prey represents highly specialized behavior. As has been shown by Krombein (1953a), this habit is associated with the wasp's inflicting on the spiders only a short span of paralysis so that the spider recovers rapidly

and moves about as before, except that it now carries the egg (and later, the larva) of the wasp.

Perhaps the best known of these wasps are the members of the genus *Homonotus*. The life history of the European species, *sanguinolentus* Fabricius, was first given (sub *Salius*) by Kryger (1910), but amplified in great detail, and with excellent illustrations, by Nielsen (1936). The host spider is *Chiracanthium carnifex* (C. L. Koch), a species which gathers blades of grasses, or leaves of heather and similar low growing plants, to construct a silken-lined retreat in which it will lay its eggs. The wasp forces its way into the retreat, stings the spider and lays an egg on the spider's abdomen. The spider's retreat thus serves as a place of concealment for the developing larva, and for the pupal cocoon. A similar account has been given by Iwata (1932, 1942) for *Homonotus iwatai* Yasumatsu parasitic on *Chiracanthium rufulum* Kishida, and excellent photographs are supplied by Yaginuma (1956) of the spider, *C. japonicum* (Bösenberg & Strand), of its nests, and of the wasp, *H. japonicus*.

A somewhat similar situation exists, as shown by Williams (1928), with the wasp *Notocyphus tyrannicus* Smith and the tropical theraphosid *Tapinauchenius*. This arboreal tarantula constructs a nest by folding leaves about five or six feet up in a tree, the same nest serving for the developing parasite too.

Hartman (1905) reported his observations in July of a pompilid attacking a spider on its web, laying an egg and then leaving the spider. The imago that emerged in late August was not identified as to species, nor was the spider identified. However, from the description of the position of the web, in a corner of the verandah, and from Hartman's account of the wasp "dragging the spider backwards over its own web" it seems probable that the spider was one of the synanthropic agelenids (e.g., of the genera *Coras, Tegenaria, Agelenopsis,* etc.) which construct a more or less horizontal sheet, over which they run in an upright (not inverted) position.

Cocoons made by a wasp of similar habits were collected by J. M. Hollister from sheet webs at Melbourne, Florida (see Cushman, 1942). Although Hollister described the webs as "sheet" rather than "funnel", implying that the spiders were not agelenids, but possibly linyphiids, it should be emphasized that the webs of some agelenids do not show the funnel very clearly. I am of the opinion that the host spiders were agelenids, or possibly even the atypical lycosid, *Sosippus floridanus* Simon, which is known to construct close-to-the-ground webs like those of the Agelenidae.

The European cribellate spider, *Eresus cinnabarinus* (Olivier),

constructs a sheet web connected to plants close to the ground, and attached by threads to a silk-lined vertical burrow extending into the ground. Bertkau (1878) reported finding in July several specimens that were parasitized, each with a larva on its abdomen. The imagines emerged from their cocoons in August and proved to be *Pompilus coccineus* Fabricius (= *Paraferreola rhombica* Christ.). In 1892 van Hasselt, in reviewing the literature on spider parasites, mistakenly reported this wasp as having been reared from the egg sacs of the spider.

Although the parasite was not reared, I believe that the hymenopter referred to by Muma (1945) was likewise a pompilid. Muma found a large pupal cocoon next to the remains of a female *Atypus bicolor* Lucas in its web.[2] As is the case in *Eresus, Atypus* constructs a vertical burrow lined with silk and has an extension of the silk (i.e., the elongated "purse" shaped portion of the web) above ground for a short distance.

From attacking spiders on their webs close to the ground it is but a short step to attacking them inside their burrows in the ground. Jenks (1938) presents a graphic account, with photographs, of the life cycle of *Psorthaspis planata* (Fox), whose host is the trap-door spider, *Bothriocyrtum californicum* (O. P.-Cambridge). The wasp enters the burrow to sting the spider and then leaves, after laying its egg on the spider's abdomen. Another ctenizid, *Aptostichus stanfordianus* Smith is parasitized by *Planiceps* (= *Aporus*) *hirsutus* (Banks), which, according to Williams (1928), first opens the trap-door, lures the spider from its burrow, stings it, drags it back into its burrow, and then leaves after placing an egg on the spider's body. In a later paper (1956) Williams reported pepsine wasps stinging, and ovipositing on, tarantulas[3] right in their shallow burrows and covering them there.

According to Evans, Adlerz (1910b) reported that the European wasp, *Pompilus* (*Anoplochares*) *spissus* Schiødte, enters the burrow of certain species of *Tarentula*,[3] stings the spider, lays its egg, then leaves and closes the entrance of the burrow. Judging from the observations of Fabre (1883) on *Pompilus apicalis* van der Lind, and (1890) on *Calicurgus annulatus* (Fabricius), as first reported by Emery (1894) and later by Sharp (1901), the closing of the burrow is a matter of merely moving into place a few loose stones from the vicinity of the burrow.

[2] Private communication.

[3] A "tarantula" is a member of the Theraphosidae, while *Tarentula* is a genus of wolf spiders (Lycosidae). In each group there are members that build shallow temporary burrows.

Lichtenstein (1869) reported collecting a spider carrying the larva of a parasite which he took for an ichneumon. The spider was not identified, but from the information supplied it was without question a ground-running form, not a snare-builder, and I would suppose it to have been a lycosid. According to Sharp the parasite was afterward ascertained to be a *Calicurgus hyalinatus* (Fabricius). Other European prey records for this wasp include *Araneus cucurbitinus* Clerck (Bristowe, 1941), and Krombein (1958) found the American subspecies *alienatus* Smith dragging a paralyzed *Neoscona* sp. It would appear, therefore, that with the closely related species of *Calicurgus* we may see displayed a variety of behavior patterns from the typical dragging of the prey to a nest the wasp will dig, or just closing up the burrow in which the wasp finds the spider, to ovipositing on a spider which is left to run about freely.

Similar variation of behavior appears to occur in *Anoplius marginalis* (Banks) which is known, for the most part, to dig a burrow. Yet Krombein (1953a) reported this species attacking a burrowing wolf spider, *Geolycosa pikei* (Marx), near the mouth of the spider's burrow, then dragging the spider into the burrow. At another time he saw the same species of wasp enter the burrow and attack the *Geolycosa* inside its burrow (1953b). Presumably the wasp is satisfied to use the burrow of its host instead of digging its own, which it can very well do.

The very first published account of an identified pompilid reared from an identified spider was that of Karsch (1872). He collected, in July, a female *Tarentula inquilina* (Clerck) which he brought into the laboratory. The spider appeared not at all disturbed by the presence of the parasite, but eventually the latter killed its host, pupated, and emerged in mid-August as a *Pompilus fuscus* (Fabricius) (= *Priocnemis trivialis* Klug?). Karsch also reviewed the data given by Menge (1866) and came to the conclusion that the latter probably had the same species of wasp, although in Menge's case the host spider was a female *Arctosa cinerea* (Fabricius). Even though Menge was unsuccessful in rearing the parasite, his drawings show the young larva with a large head and narrow neck, somewhat as in the drawings of my specimen (Figs. 3 and 4), and show the older larva with a much less conspicuous head. It was certainly not a dipteron, as Menge supposed. Adlerz (1910a), reviewing the literature, agreed with Karsch.

Lichtenstein and Rabaud (1922) cite this type of parasitic habit as "accidental" for pompilids, though usual for *Polysphincta*. I

have searched the literature and my own records, and am unable to find a single instance of dipterous parasitism where the larva is *external,* nor a single instance of a polysphinctine ichneumon reared from a lycosid. I feel, therefore, that it is safe to assume that not only was Menge's parasite a pompilid, but so also were those reported from a *Lycosa* by Sanborn (1871), who thought he had a dipteron, and from a *Pardosa luteola* Marx (= *hyperborea* Thorell) by Howard (1892), who thought he had a *Polysphincta.*

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